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STERNAL GLANDS IN THREE SPECIES OF MALE SOCIAL WASPS OF THE GENUS *MISCHOCYTTARUS* (HYMENOPTERA: VESPIDAE)

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Abstract.—Males of *Mischocyttarus flavitarsis* and *M. drewseni* possess a large mass of ducted exocrine gland cells on each of the fifth, sixth, and seventh (terminal) gastral sternites. The epidermal cells in the region of these glands are elongated, suggesting that they also have a secretory function. Males of a third species, *M. mexicanus,* have relatively few ducted gland cells on the fifth and sixth sternites and none on the seventh sternite. In *M. flavitarsis* (but not in *M. drewseni* or *M. mexicanus*), the gland cell ducts of sternites five and six open into a dense brush of long hairs.

Mischocyttarus, even though it is strictly New World in distribution, is the largest genus of social wasps (Richards 1978). Recent studies of four species reveal a diversity of male mate-locating behavior within the genus. Males of *Mischocyttarus labiatus* (F.) in Colombia, *M. mexicanus* (de Saussure) in Florida, and *M. drewseni* de Saussure in Brazil patrol routes in areas where females converge to feed or to nest (Litte 1981; personal communication; Jeanne and Castellón Bermúdez 1980). The males of *M. flavitarsis* (de Saussure) in Arizona pursue two different strategies, depending on the season: during the summer nesting season they patrol routes in female foraging areas, but in the fall, during dissolution of the colonies prior to hibernation, they defend small territories near hibernation sites (Litte 1979). Males of *M. labiatus* and *M. flavitarsis* drag and rub the gaster on perch sites, as though scent-marking (Litte 1981, 1979), while *M. mexicanus* and *M. drewseni* evidently lack this behavior (Litte, personal communication; Jeanne and Castellón Bermúdez 1980). Landolt and Akre (1979) reported that a *M. flavitarsis* male from Washington State possessed large glandular masses on the sixth and seventh (terminal) gastral sternites. The glands are probably the source of a secretion which the male applies to his perch (Litte 1979). However, the roles of this behavior and of any pheromone that may be deposited remain to be determined.

These behavioral observations suggest differences in the occurrence of sternal glands among these species. The purpose of this paper is to determine the presence of these glands and to describe their morphology in males of three of the species: *M. flavitarsis, M. drewseni,* and *M. mexicanus.* This is the first study of the histology of exocrine glands in male social wasps.

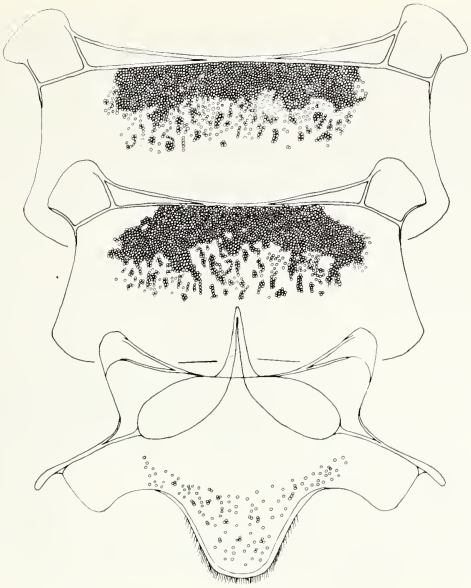


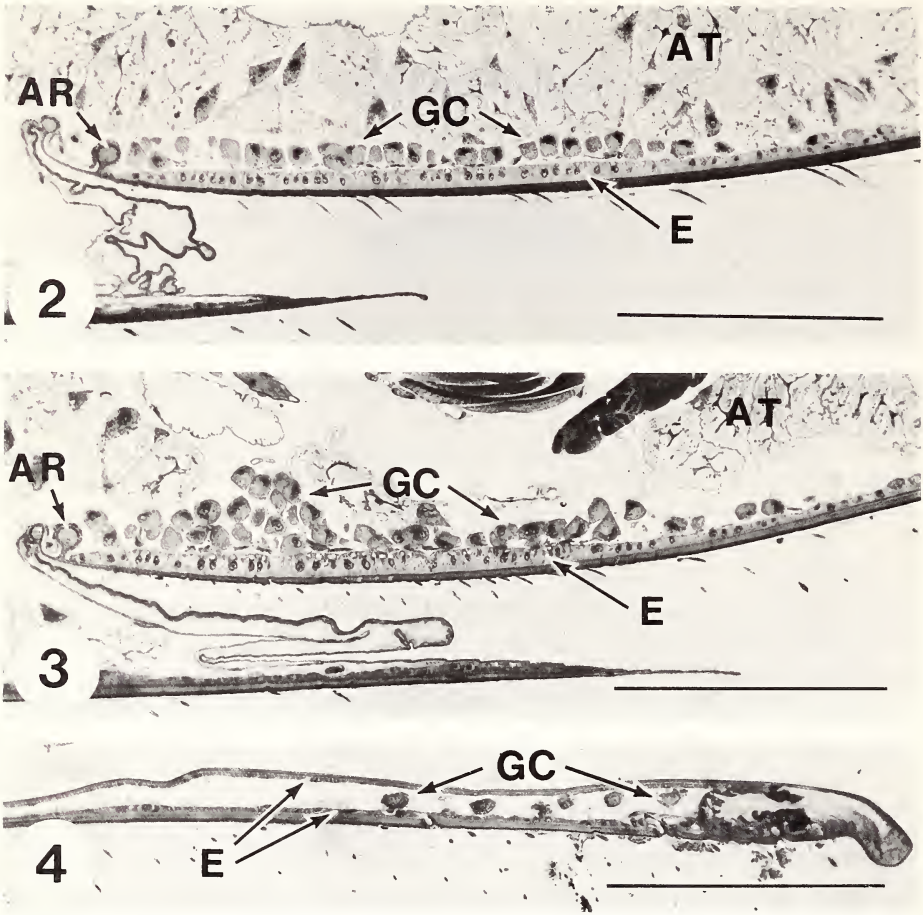
Fig. 1. Location of the class 3 gland cells on the fifth, sixth, and seventh gastral sternites of the male of *M. drewseni*.

Methods

Adult males of each species were collected from the localities of the behavioral studies cited above, as follows. *M. flavitarsis navajo* Bequaert: near the Southwestern Research Station, Portal, Arizona (fall of 1959 and 1978); *M. mexicanus* (de Saussure): Archbold Biological Station, Lake Placid, Florida (early spring of 1980); *M. drewseni* de Saussure: Fazenda Taperinha, Santarém, Pará, Brazil (November, 1978). *M. f. flavitarsis* (de Saussure) from Turlock, California, was examined with SEM for comparison with *M. f. navajo*.

Specimens were fixed in Kahle's solution, embedded in Spurr Low-Viscosity embedding media (Polysciences), and sectioned 2 μ thick for examination with a light microscope (Post and Jeanne 1980). Specimens were prepared for scanning electron microscopy as described by Post and Jeanne (1980) and examined with a JELCO JSM-U3 scanning electron microscope.

The glands of each species differ from one another only in relative size. For this reason we illustrate the fifth (antepenultimate), sixth (penultimate), and seventh (terminal) gastral sternites of *M. drewseni* and discuss the other species in relation to it.



Figs. 2–4. Longitudinal section (2 μ thick) through the glandular area of the fifth, sixth, and seventh gastral sternites of *M. drewseni*. 2. Fifth sternite. 3. Sixth sternite. 4. Seventh sternite. Anterior to left. AR = anterior ridge; AT = adipose tissue; E = epidermal cells; GC = glandular cells; Scale = 0.25 mm.

Results

Internal Anatomy

A broad, dense mat of individually ducted gland cells (''class 3 cells'' of Noirot and Quennedey 1974) underlies the anterior margin of each of sternites 5 and 6 in *M. drewseni* (Figs. 1–4). The duct of each cell passes through the integument to open onto the surface of the sternite (Fig. 5). The gland cell mass on the fifth sternite measures 1.9 mm wide by 0.6 mm front to rear

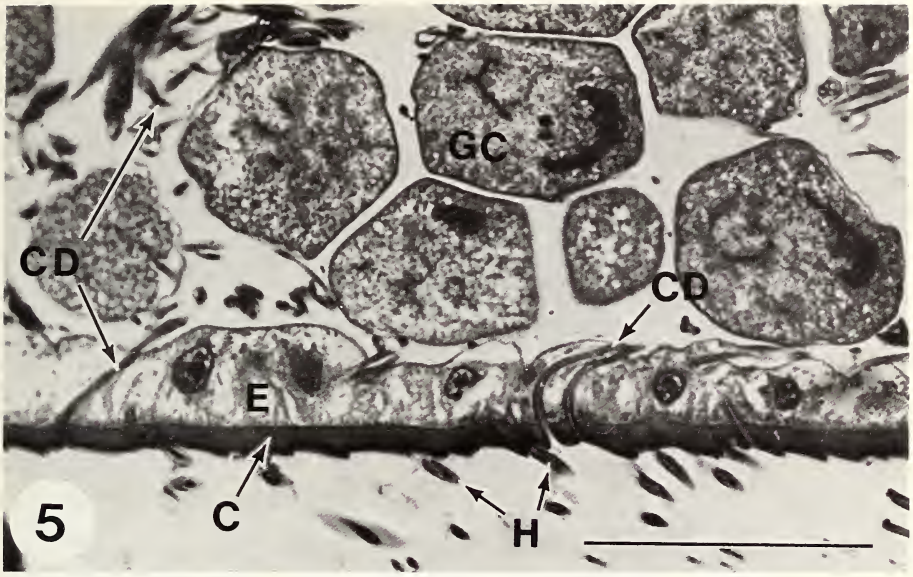


Fig. 5. Longitudinal section (2 μ thick) through the glandular area of the sixth gastral sternite of *M. flavitarsis navajo*. C = cuticle; CD = glandular cell ducts; E = epidermal cells; GC = glandular cells; H = hairs of the sternal brush. Scale = 0.05 mm.

and is a single cell layer thick (ca. 0.025 mm) (Fig. 2). In contrast the mass on the sixth sternite is 1–3 cells thick (Fig. 3) and greater in extent (2.0 mm by 0.7 mm). The seventh sternite has only scattered class 3 cells underlying its posterior half (Figs. 1, 4). In one specimen there were 115 cells.

The location of class 3 cells on each sternite is the same in *M. flavitarsis navajo* as in *M. drewseni,* but the cells are more numerous. The masses of cells extend the full width of sternites 5 and 6 (2.8 and 2.6 mm, respectively) and are somewhat bilobed, measuring, respectively 0.8 mm and 0.9 mm along the midline and 1.0 mm and 1.1 mm on the sides. Both masses of cells are also thicker than in *M. drewseni*: that on the fifth is 2–4 cells thick, while that on the sixth is 2–8 cells thick (both glands are thinner at the edges). The class 3 cells on the seventh sternite form a dense mat, one cell thick, comprising about 300 cells in one specimen.

In contrast, *M. mexicanus* has only a few scattered class 3 cells on the anterior margins of sternites 5 and 6. In one specimen there were 73 and 48 cells on the two sternites, respectively. The seventh sternite lacks class 3 cells.

In all three species the epidermal layer is thickened in the region of the class 3 cells, suggesting that these cells are actively secreting ("class 1 cells" of Noirot and Quennedey 1974) (Figs. 2–4). The layer is much thicker

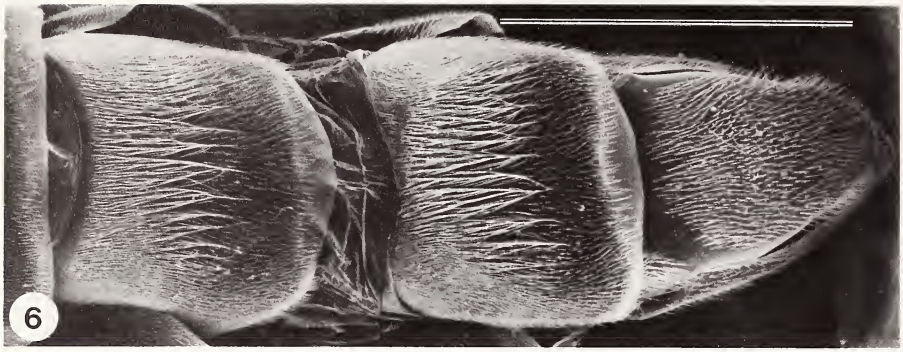


Fig. 6. SEM photograph of the fifth, sixth, and seventh (terminal) gastral sternites of *M. f. navajo*. Sternites are pulled apart to expose their anterior margins. Scale = 2.0 mm.

in *M. drewseni* ($\bar{x}$ = 27.0 μ; SD = 9.5 and $\bar{x}$ = 33.9 μ; SD = 16.1 on the fifth and sixth sternites, respectively; 3 specimens) than in *M. f. navajo* ($\bar{x}$ = 20.6 μ; SD = 4.2 and $\bar{x}$ = 21.9 μ; SD = 6.4 on the fifth and sixth sternites, respectively; 3 specimens). The epidermal cells of *M. mexicanus* are not highly modified on these two sternites (6.7 μ thick; 1 specimen). On the seventh sternite the elongation is greater in *M. f. navajo* ($\bar{x}$ = 24.9 μ; SD = 3.4; 3 specimens) than in *M. mexicanus* (15.5 μ; 1 specimen) and *M. drewseni* ($\bar{x}$ = 11.1 μ; SD = 0.3; 2 specimens).

External Morphology

The anterior regions of both the fifth and sixth gastral sternites of *M. flavitarsis navajo* (6 specimens) and *M. f. flavitarsis* (2 specimens) males are densely covered with long, brush-like hairs, while the seventh sternite lacks these (Fig. 6). All three sternites of *M. drewseni* (3 specimens) and *M. mexicanus* (3 specimens) lack these hairs, and resemble the seventh sternite of *M. flavitarsis*.

Glandular duct openings are located between the long hairs of *M. f. navajo* (Figs. 5, 7) and between the body hairs of *M. drewseni* (Fig. 8) and *M. mexicanus*.

Discussion

Landolt and Akre (1979) report sternal bushes and ducted, globular gland cells on the sixth and seventh gastral (seventh and eighth abdominal) ster-

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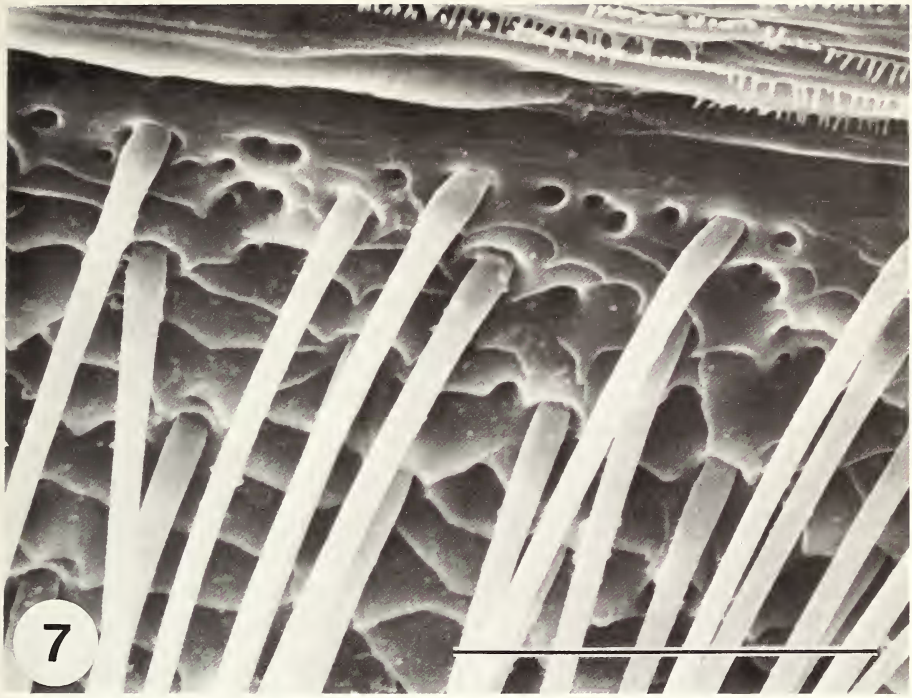
Figs. 7–8. SEM photograph of the glandular cell duct openings (seen as pores) near the base of the fifth gastral sternite. 7. *M. f. navajo*. 8. *M. drewseni*. Scale = 0.05 mm.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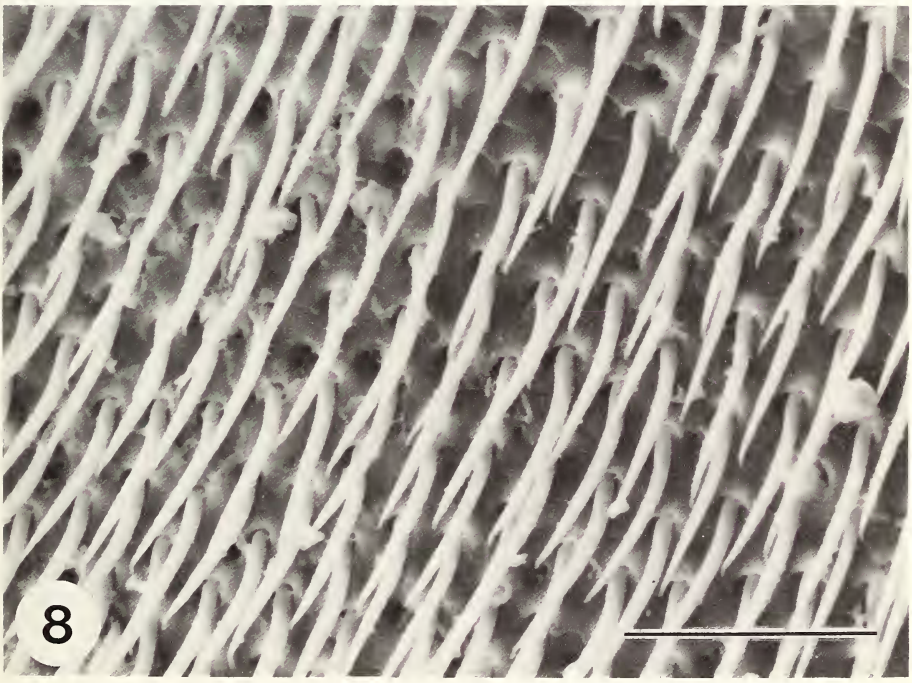
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nites of a male of *M. flavitarsis* from Washington State (probably *M. f. idahoensis* Bequaert). Our specimens of *M. f. navajo* from Arizona and *M. f. flavitarsis* from California clearly have these structures on gastral sternites 5 and 6. Either Landolt and Akre were in error or the subspecific difference is real. We were unable to obtain specimens of *M. flavitarsis* from Washington State, so we cannot resolve the question.

Since the number of gland cells is fixed in the adult stage, the observed differences in the number of class 3 gland cells are species differences and cannot be attributed to developmental differences. Of the three species we examined, *M. flavitarsis navajo* has the greatest number of class 3 gland cells on all three sternites and is the only species with sternal brushes. It also appears to be the only one of the three whose males rub these sternites on the substrate (Litte 1979; personal communication; Jeanne and Castellón Bermúdez 1980). A sternal brush appears to be a common structure in species of aculeate wasps known to rub a secretion onto a substrate, for example males of *Eucerceris* spp. and *Philanthus* spp. (Alcock 1975; Gwynne 1978; O'Neill 1979), and females of *Polistes* spp. (Hermann and Dirks 1974; Turillazzi 1979; Post and Jeanne 1980) and *Mischocyttarus* spp. (Jeanne 1970). These facts suggest the possibility that the 5th and 6th sternal glands serve different functions in *M. drewseni* and *M. mexicanus* than in *M. flavitarsis*. The location of the class 3 gland cells on the posterior half of sternite 7 in *M. flavitarsis* and *M. drewseni* suggests that their role is different from that of the cells on the preceding two segments.

The differences in height of the thickened epidermal cells may reflect only developmental differences. Since we had no information about age or activity of the specimens we sampled, all we can say is that in all three species these cells appear to be glandular in function.

This study reveals that species in the genus *Mischocyttarus* are not uniform with respect to the occurrence and size of male sternal glands. It is likely that further diversity will be found among the remaining 199 species. Our results, combined with the behavioral studies already completed, strongly suggest interspecific differences in the importance of chemical signals in the behavior of males, either on the natal nest, in a reproductive context, or both.

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